Divergence-time estimates for hominins provide insight into encephalization and body mass trends in human evolution

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Hans P. Püschel[1]*, Ornella C. Bertrand[1], Joseph E. O'Reilly[2], René Bobe[3,4], Thomas A. Püschel[3]*

1 School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh, EH9 3FE, Scotland, United Kingdom.

2 MRC Human Genetics Unit, MRC Institute of Genetics & Molecular Medicine, University of Edinburgh, Western General Hospital, Crewe Road, Edinburgh, EH4 2XU, Scotland, United Kingdom.

3 Primate Models for Behavioural Evolution Lab, Institute of Cognitive and Evolutionary Anthropology, School of Anthropology, University of Oxford, 64 Banbury Road, Oxford, OX2 6PN, England, United Kingdom.

4 Gorongosa National Park, Sofala, Mozambique.

*Corresponding authors:

Hans P. Püschel

E-mail: H.P.Puschel-Rouliez@sms.ed.ac.uk

Phone: +44 (0) 7741054298

Thomas A. Püschel

E-mail: thomas.puschelrouliez@anthro.ox.ac.uk

Phone: +44 (0) 7476608464

Abstract

Quantifying speciation times during human evolution is fundamental as it provides a timescale to test for the correlation between key evolutionary transitions and extrinsic factors like climatic or environmental change. Here we applied a Total Evidence Dating approach to a hominin phylogeny to estimate divergence times under different topological hypotheses. The time scaled phylogenies were subsequently used to perform ancestral state reconstruction of body mass and phylogenetic encephalization quotient (PEQ). Our divergence time estimates are consistent with other recent studies that analysed extant species. We show that the origin of *Homo* most likely occurred between 4.30 and 2.56 Ma. The ancestral state reconstructions show a general trend towards a smaller body mass before the emergence of *Homo*, whilst followed by a trend towards a greater body mass. PEQ estimations display a general trend of gradual but accelerating encephalization evolution. The obtained results provide a rigorous temporal framework for human evolution.

Introduction

Establishing an evolutionary timescale for human evolution is of essential relevance in palaeoanthropology[1–3] because reliable estimates of the timing of speciation events across the hominin phylogeny facilitate the correlation of these events with both abiotic and biotic processes on geological timescales. An accurate timescale also provides a framework to test for associations between landmark evolutionary changes and different putative extrinsic causal factors such as changes in climate or other environmental influences[4,5]. Despite recent relevant fossil findings, the antiquity and emergence of the genus *Homo*, as well as the timing of the divergence of our lineage with other African apes have not found a consensus[6–9].

Traditionally, palaeoanthropologists have employed maximum parsimony analysis to infer hominin phylogenetic relationships[10–12], but this approach does not explicitly estimate

45 divergence-times as part of the estimation of the phylogeny. Previous studies[13,14] computed
46 confidence intervals for the disappearances and appearances of several hominins. However,
47 their approach is not easily applicable to several available hominin taxa, as it requires the
48 availability of extensive palaeontological datasets. Additionally, this method only provides
49 confidence intervals for local first and last appearance data, which do not correspond to the
50 global origination and extinction dates of the taxa under analysis. Other studies have
51 computed these values but their results have been limited by either focusing on a restricted
52 number of hominin taxa[2] or because the assumptions of their applied methods were not met[15].
53 Bayesian phylogenetic inference methods have also been applied to morphological data[16,17] to
54 provide divergence time estimates. However, these estimates were exclusively based on
55 anatomical data, even though it is now widely known that the fragmentary nature of the fossil
56 record is not enough to compute reliable divergence estimates[18], and that it is necessary to
57 consider the molecular information available for several hominin and ape taxa in the
58 analyses.

59 There is currently a consensus that the most feasible way of determining an accurate
60 evolutionary timescale is by using the molecular clock, a prospect that has progressively
61 concretised with the development of Bayesian relaxed clock methods[19–22]. Bayesian
62 divergence-time estimates require the use of prior probability distributions to incorporate
63 fossil evidence for calibrating the tree. Recently, a new approach known as 'total-evidence
64 dating' (TED), 'tip-dating' or 'integrative dating'[23] has been developed[24,25]. TED
65 complements the molecular sequence data derived from extant species with morphological
66 information from both living and extinct species, which allows a more thorough inclusion of
67 fossil data in the analysis and estimation of divergence-times.

Hence, in this work we applied this divergence-time estimation method to produce total evidence evolutionary timescales for the hominin clade. We considered four different topological hypotheses with alternative reasonable affinities for problematic hominin taxa (Fig. 1). This is highly relevant because these timescales can be used for dating the origin of *Homo* or any other hominin genus, inferring evolutionary rates and patterns, as well as providing a better understanding of the coevolution of hominins and their environment. Additionally, we subsequently used the dated trees to carry out ancestral state reconstruction (ACSR) of two evolutionary important phenotypic characters: body mass and phylogenetic encephalization quotient (PEQ). Body mass impacts almost every aspect of an animal's biology and ecology[26,27], hence its importance in any palaeobiological inference, whilst an evolutionary trend of increasing encephalization is one of the hallmark processes in human evolution[28,29].

Results

The TED analyses (Fig. 2, Extended Data Fig. 1 and Table 1) show, in general, better-resolved divergence times for the nodes that have both morphological and molecular information available, in comparison with the nodes estimated with morphological information alone. The common ancestor of hominins and *P. troglodytes* (node 2) was dated at around 7.5 Ma with an uncertainty range of 8.59 – 6.61 Ma considering the 95% highest posterior density intervals (HPD) of all the trees. The common ancestor of the genus *Homo* (node 13 or 14 for *H. floresiensis* hypothesis) was dated at around 3.3 Ma with an uncertainty range of 4.30 – 2.56 Ma considering the 95% HPD of all the trees. In general, estimations for this node were consistent between the four trees, although the biggest difference resulted when *H. floresiensis* is removed from the base of *Homo*, making the node's age slightly younger (Fig. 2d). The prior sensitivity analysis (Extended Data Fig. 2) shows mostly minor

92 differences between divergence-times in the original analysis and analyses using different
93 priors in relevant parameters, suggesting that the TED analyses are robust to changes in the
94 employed priors.

95 The maximum likelihood (ML) ACSR based on the four consensus trees (Figs. 3, 4,
96 Extended Data Figs. 3-6) are consistent with the ACSR based on samples of the posterior
97 trees from these analyses (Fig. 5 and Extended Data Fig. 7). The main difference is an
98 apparent PEQ overestimation in the case of the ACSR based on the consensus trees versus
99 the ACSR based on samples of the posterior trees (Fig. 5). These differences are explained
100 because using equations based on PGLS regressions of the consensus trees (Extended Data
101 Fig. 8) returned lower expected brain masses calculated for the trees' tips on average than
102 equations based on the sampled trees (Extended Data Fig. 9). However, the general PEQ
103 trends remain the same. Similarly, the brain mass ACSR versus body mass ACSR regressions
104 results show a consistently similar pattern for the four analyses. When we analyse all the
105 nodes together in the four trees, the slopes are slightly positive and the R^2 values are low
106 (around 0.11) (Extended Data Fig. 10a-d). However, when we split the data there are clearly
107 two different trends. Before node 13/14 the slopes are negative with a moderate R^2 (around
108 0.46) (Extended Data Fig. 10e-h), whereas after node 13/14 the slopes are strongly positive
109 with a high R^2 (around 0.96) (Extended Data Fig. 10i-l).

110 The speciation events that occurred since the divergence from *G. gorilla* to the common
111 ancestor of *Homo* (nodes 1-9 and 13/14), all occurred within the latest Miocene and Pliocene
112 (Fig. 2 and Table 1). For that period, the body mass ACSR show that from a common
113 ancestor of around 71 kg at 10.4 Ma, there is a trend of rapid decrease in body mass reaching
114 around 38 kg by 3.3 Ma (Figs. 3, 5a-d, and Extended Data Fig. 5). That is 1.87 smaller in 7.1
115 Myr. However, the PEQ ACSR show an opposite trend, increasing from around 0.87 to 1.88

in the same period (Figs. 4, 5e-h and Extended Data Fig. 6), which is 2.16 times greater. The effect of removing of *H. floresiensis* from the base of *Homo* (Figs. 4d, 5h and Extended Data Fig. 6d) is a higher estimated PEQ for the last common ancestor of this genus (i.e., 2.16) and the surrounding nodes. Following the path leading to *Au. africanus* and the members of the genus *Paranthropus* (nodes 1-10) the body mass tends to decrease to around 37 kg at node 10, which means a reduction of 1.92 times from the root in 6.6 Myr. Nevertheless, the path from nodes 9 to 10 does not indicate an increase in PEQ. Instead, it corresponds to the beginning of a slight reduction in PEQ in the lineage leading to *Paranthropus*. Interestingly, the last member of this genus*, P. robustus*, displays an increase in PEQ just before the extinction of the lineage. The incorporation of *Au. sediba* as the sister taxon of *Au. africanus* did not have a substantial influence on the ACSR of the neighbouring nodes.

Speciation events since the common ancestor of *Homo* start to occur around the mid-Pliocene at 3.3 Ma and end around the mid-Pleistocene at 0.6 Ma (Fig. 2 and Table 1). In contrast to the previous decreasing trend in body mass, the body mass ACSR show an increment from around 38 kg to 65 kg in this period (nodes 13/14-24; Figs. 3, 5a-d, and Extended Data Fig. 5). This corresponds to an increase in body mass of 1.71 times in 2.7 Myr, which means a reversion in body size to similar levels as the one observed at the tree's root but in less than half of the time. In other words, the rate of body mass evolution approximately doubled in the genus *Homo* from what has been previously seen (10.0 kg/Myr vs 4.6 kg/Myr). However, these increments were not equal in all nodes and some groups even show a body mass reduction. For instance, the parallel branch that goes from node 14 to *Homo habilis* shows a decrease in body mass regardless of the position of *Au. sediba*. The effect of removing *Au. sediba* from *Homo* results in a slight increase in the reconstructed body mass at node 14. Similarly, *H. floresiensis* and *H. naledi* also displayed a considerable decrease in body mass from their ancestors in all the hypotheses. However, the decrease and its rate vary with the

different hypotheses. When *H. floresiens*is is positioned at the base of *Homo*, the decrease is around 10 kg (-3.0 kg/Myr), while when it is considered the sister taxon of the Asian *H. erectus* the decrease is approximately 22 kg (-13.0 kg/Myr). When *H. naledi* is at the stem of *H. antecessor* the decrease is around 13 kg (-10.1 kg/Myr), whereas when it is the sister taxon of the African *H. erectus* the decrease is approximately 5 kg (-3.0 kg/Myr).

The PEQ ACSR for the period since the common ancestor of *Homo* (node 13/14) keeps the previously observed increasing trend, augmenting 1.53 times in 2.70 Myr, from around 1.88 in node 13/14 to 2.88 in node 24 (Figs. 4, 5e-h and Extended Data Fig. 6). Even though the increase in PEQ is similar with the PEQ evolution before the common ancestor of *Homo* (1.00 and 1.01 respectively), its rate increased 2.64 times, going from 0.14 PEQ/Myr to 0.37 PEQ/Myr. Within this general PEQ evolutionary trend, there are three taxa that stand out from the rest: *H. floresiensis*, *H. naledi* and *H. sapiens*, although in the first two species the specific trends vary with the different hypotheses. When *H. floresiensis* is positioned is at the base of *Homo*, it displays a slight decrease or stasis in PEQ from its ancestor exhibiting a value around 1.7 for 3.4 Myr of evolutionary history, while when it is considered the sister taxon of the Asian *H. erectus* the decrease is 0.52 in 1.7 Myr (-0.30 PEQ/Myr). When *Homo naledi* is at the stem of *H. antecessor*, the PEQ decreases around 0.85 in 1.3 Myr (-0.65 PEQ/Myr), whereas when it is the sister taxon of the African *H. erectus* the decrease is approximately of 0.69 in 1.7 Myr (-0.42 PEQ/Myr). This strong decrease under different scenarios puts *H. naledi* very close to the PEQ values for *Au. afarensis*. In contrast, *H. sapiens* stands out due to its rapid increase in PEQ from its common ancestor with *H. neanderthalensis* (node 24), going from around 2.88 to 3.22 in approximately 0.55 Myr. That is 0.62 PEQ/Myr, which is 1.68 times greater compared to the rate observed since the common ancestor of *Homo* (nodes 13/14 to 24) between 3.3 Ma and 0.6 Ma, and 4.43 greater

in comparison to the rate observed since the common ancestor of *G. gorilla* and the ancestor of *Homo* (nodes 1 to 13/14) between 10.4 Ma and 3.3 Ma.

Discussion

We have presented here TED estimates of the divergence-times of most hominin taxa under different hypotheses. Our divergence estimates are in general agreement with previous molecular studies using fossil node-calibrations[30–34], as well as with fossil calibration independent methods, such as those using generation times[35]. The topology of our trees (Fig. 2) differs from the trees of Dembo *et al*[16,17] in the position of *H. neanderthalensis* relative to *H. sapiens* and *H. heidelbergensis*, which is likely due to the influence of the mtDNA in our Total Evidence analysis. The position of these groups plus Denisovans is the same as obtained in a previous study[34] using mtDNA but differs from studies using nuclear DNA[36], probably related to a mtDNA introgression event that occurred ~270 ka[37]. We think our divergence-time estimates are robust and consistent with the current evidence available. However, further refinements in some of the fossilized birth-death (FBD) model's assumptions, namely being able to consider a nonuniform fossil sampling among clades[38], and new fossil discoveries, could further improve these estimates.

Our ACSR results from the four different considered hypotheses are consistent between them, showing that refining the phylogenetic affinities of problematic taxa (e.g., *H. naledi*) would probably have a minor impact in major body size and encephalization trends in hominin evolution. Furthermore, our ACSR results are consistent with previous studies that show that body size in hominins has not been a simple linear increment since the divergence with *P. troglodytes*[26,27,39]. The observed decreasing trend in body size from the root of the tree is in agreement with previous studies that suggest a chimpanzee-sized common ancestor

189 with *P. troglodytes*[40,41]. Our ACSR results also displayed a general trend towards greater
190 body size that started after the emergence of the last common ancestor of *Homo*, contrary to a
191 previous claim stating that there were no clear body mass temporal trends in hominin
192 evolution[26]. Instead, our results showed a complex history of body size changes that do not
193 correlate linearly with brain size changes. It may be that after the emergence of the genus
194 *Homo*, brain size carried body size increases as previously suggested[42] (Extended Data Fig.
195 10i-l). However, before the emergence of *Homo*, brain size and body size seem to be
196 decoupled or following opposite directions (Extended Data Fig. 10e-h). Our results also agree
197 with Pagel's[43] seminal work and other studies (e.g.,[44–46]) that showed a general trend of
198 gradual but accelerating brain size evolution in hominins. However, some of them (i.e.,[44,45])
199 directly analysed endocranial volume without taking into account body mass estimations,
200 which we considered in our PEQ estimations. This is problematic because it is only when
201 body size is considered[47] and phylogeny is included that we can consider whether observed
202 brain size differences are significant in terms of encephalization[28,48,49]. We are confident that
203 our ACRS are reliable and consistent with the current evidence. Nevertheless, it is important
204 to note that the inclusion of more fossils near the root could have an impact in the ACSR, in
205 particular for the oldest nodes of the tree. Additionally, ACSR could be affected by the use of
206 different methods and models of character evolution[50].

207 The fact that PEQ evolution tends to accelerate when moving from a relatively stable climate
208 to more unstable climatic conditions (Fig. 2) appears to agree with the 'variability selection'
209 hypothesis which correlates major adaptations in hominins with periods of high climatic
210 variability[51,52]. Before the emergence of *Homo*, hominin evolution occurred in a mostly warm
211 period although with a global cooling trend, which had started after the Mid-Miocene
212 Climatic Optimum and the recovery of Antarctic ice-sheets around 10 Ma[53]. From a common
213 ancestor with *P. troglodytes* at around 7.5 Ma, bipedalism started to emerge at least by 6

Ma[54–57] in the hominin lineage. This relatively stable period was interrupted by considerable temperature oscillations around the Miocene/Pliocene boundary at 5.3 Ma. Subsequently with the development of 23 kyr dominant glacial cycles, we observed the emergence of the genus *Homo* and an evolutionary shift, displaying the end of a general trend towards smaller body size and the beginning of an acceleration of the increase in PEQ and the start of a general trend towards larger body masses (Figs. 2-4). Even though the earliest member of *Homo* discovered so far was from 2.8 Ma[58], our analysis allows us to predict the presence of early representatives of the *Homo* lineage not yet found (or identified) in the African fossil record around 3.3 Ma (i.e., 0.5 Myr earlier). Interestingly, 3.3 Ma is the age attributed to stone tools discovered in West Turkana[59], which are commonly associated with *K. platyops*[60] and *Au. afarensis*[61].

After the Pliocene-Pleistocene boundary at 2.58 Ma, the trend towards cooler temperatures and aridity continues, and 41 kyr dominant glacial cycles are established, with an intensification of climatic fluctuations. As PEQ continues to increase, so does the evidence of increasingly complex behaviours: tool innovations (Oldowan [2.6 Ma[62]], Acheulean [1.7-1.4 Ma[63]] and Aurignacian at [120–~50 ka[64]], the use of fire (from 1.5 Ma onwards[65,66] [strong evidence at 1.0–0.5 Ma[67]]), cooking and more frequent meat consumption[68–70] and the ability to produce art at ~540–430 ka[71]. By 300 ka Africa was inhabited by at least three *Homo* species, *H. sapiens*, *H. heidelbergensis* and *H. naledi*, and Eurasia by *H. neanderthalensis*, Denisovans, *H. floresiensis*, *H. luzonensis* and also possibly *H. erectus* and *H. heidelbergensis*[72]. *H. sapiens* is the hominin species with the highest PEQ, so a possible explanation for its exclusive continuation would be that this difference in PEQ allowed *H. sapiens* to outcompete its contemporary relatives[47,73–75]. Even though it has been recently established that there was not a unique 'Out of Africa' event in *H. sapiens* history[76–79], it is widely accepted that Neanderthals were eventually displaced by *H. sapiens* in Europe by ~39

239 ka[80]. However, it is now understood that *H. neanderthalensis* was capable of very complex
240 human behaviours[81,82].

241 Like *H. sapiens*, *H. neanderthalensis* was certainly a cultural niche constructor[83–85] under
242 harsh glacial-interglacial temperature fluctuations[86]. Nonetheless, *H. sapiens* not only
243 displays a higher PEQ, but also a higher rate of change in PEQ compared to *H.*
244 *neanderthalensis*. This probably means that within Hominini, PEQ selection was particularly
245 strong within and between the metapopulations of *H. sapiens*[87] in an arid-moist fluctuating
246 Africa[86]. A larger relative brain mass has been associated in mammals with behavioural
247 flexibility, adaptation and resilience in variable environmental conditions[88]. Therefore in spite
248 of the fact that the behavioural gap between the two species may have been minimal, even a
249 small advantage in terms of behavioural flexibility and ability to adjust in a variable
250 environment as it was during the late Pleistocene[89], could have had enormous benefits in
251 terms of fitness and successful competition for *H. sapiens*[90,91]. A similar explanation could
252 also be applied for the demise of the rest of our contemporaneous relatives exhibiting an even
253 lower PEQ.

254 Considering the evolution of *H. floresiensis*, it seems that selection was acting on body size
255 by means of heterochrony[92,93] favouring a reduction in body size as a mean of decreasing the
256 energetic expenditure in a small island environment with limited resources as it also probably
257 occurred for *Stegodon florensis*[94–96]. However, our results show that resolving the
258 phylogenetic affinities of *H. floresiensis* would have important implications for the
259 evolutionary trends on this taxon. The body size reduction in *H. floresiensis* is more
260 spectacular if this taxon derives or is considered closely related to Asian *H. erectus*[97], a
261 scenario that also implies a notorious encephalization reduction. Nevertheless, more recent
262 studies favour the position of *H. floresiensis* at the base of *Homo*[16,17,98], which would then

favour a encephalization stasis scenario. Interestingly, if tool development can be associated with a certain level of cognition, considering the tools attributed to *H. floresiensis*[99,100], we anticipate that the common ancestor of *Homo* with a similar PEQ value, was most likely able make stone tools as well.

Previous studies have described *H. naledi* as a small bodied and small brained hominin of the genus *Homo*[101], with cranial[102], endocranial[103] and postcranial features[104,105] that support this placement. There are two hypotheses which attempt to explain this small brain as either a (1) retention from the common ancestor from the genus *Homo*, or (2) a reduction from a later big-brained form of *Homo*[103]. The PEQ trends displayed by *H. naledi*'s ACSR supports the second hypothesis because there is an extraordinary reduction in PEQ from a big-brained ancestor in a relatively short time, although this reduction is faster if *H. naledi* is at the stem of *H. antecessor* as previously suggested[17]. *H. naledi* lived between 236 ka and 335 ka[106] in South Africa, with a PEQ around 1.5, which is really close to *Au. afarensis* and other australopiths. This happened at a time in which big bodied and big brained hominins were the norm in continental landmasses, like *H. sapiens* and *H. neanderthalensis* both with a PEQ over 2.7. Even the insular small sized *H. floresiensis* had a higher PEQ. In a context of increasing PEQ over the hominin lineage at that time, the PEQ reduction in *H. naledi* could perhaps be explained, by the specialization in a niche of scarce and/or low energy food resources in which an expensive large brain would be prejudicial. Hypotheses in relation to the cost of encephalization like the 'expensive tissue'[107,108] and the 'energy trade off' hypotheses[109], could potentially explain this trend in *H. naledi*. Less energy expenditure could also explain the considerable body size reduction observed in *H. naledi* from its reconstructed bigger-brained ancestors. In fact, through dental topography comparisons it has been suggested that *H. naledi* was occupying a distinct ecological niche, which was different from previous and contemporaneous hominins[110].

In conclusion, our TED analyses and ACSR results showed that (1) the last common ancestor of the genus *Homo* most likely appeared around 3.3 Ma (between 4.30 and 2.56 Ma) with a body size close to that of *Au. afarensis* and an encephalization very similar to *H. floresiensis*, (2) hominin body mass evolution followed a general decreasing trend before the emergence of *Homo* and exhibited a general increasing trend afterwards, (3) hominins displayed a general trend of gradual but accelerating encephalization through time.

Methods

Data collection and Total Evidence analyses

We used TED analyses which are a collection of Bayesian phylogenetic methods (see[111] for a general primer and [19,20,22,112,113] for reviews of Bayesian molecular dating methodology). For the TED analysis, our taxon sampling was similar to previous published analyses[17] but Denisovans were also included. The morphological data were obtained from the same study[17], and comprised a supermatrix of 391 craniodental characters from matrices used in 13 previous studies[114–126]. Even though there are more recently published hominin phylogenetic analyses computed using different morphological matrices[127,128], the morphological matrix used here[17] is the most complete, to our knowledge, in terms of the number character states and hominin species included.

The molecular data were complete mtDNA genomes extracted from GenBank for the species for which it was available: *Gorilla gorilla* (KF914214.1), *Pan troglodytes* (JF727180.2), *Homo heidelbergensis* (KF683087.1), *Homo neanderthalensis* (MK123269.1), *Homo sapiens* (KC417443.1) and Denisovans (KX663333.1). Following previous analyses[34,129], we removed the D-loop region from the mtDNA due to the differential rate at which it acquires substitutions. We aligned the sequences with the MUSCLE algorithm in MEGA X[130]. Then, we analysed the alignment using PartitionFinder2[131] using the "greedy" algorithm[132], in order

312 to select the most appropriate models of molecular evolution for the different protein coding
313 and non-coding regions of the mtDNA. The best partitioning scheme on the basis of AICc
314 score included 16 partitions for the mtDNA (Supplementary Table 1). We used these
315 partitions for the mtDNA sequences, and the Mkv+ Γ model[133] for the morphological data,
316 unlinking the model parameters across these partitions. In order to avoid a mismatch in our
317 model, we used the dates associated with our data following the recommended procedure[134],
318 which meant that we did not necessarily calibrate a tip using the oldest or first fossil
319 occurrence for a particular taxon. Hence, we calibrated the fossil tips of the tree using the age
320 of the fossil specimen used for coding morphology in taxa without mtDNA available. In taxa
321 with mtDNA sequences available, the sequences were selected from individuals aged equally,
322 or as close as possible, to the morphologically coded fossils, and the age associated with
323 these sequences was used to calibrate the fossil tips. We also considered radiometric age
324 uncertainties using a uniform distribution between the maximum and minimum estimated
325 ages for each fossil when available[112] (further information can be found in Supplementary
326 Table 2).

327 The selected outgroup was *Gorilla gorilla* and the root of the tree was calibrated using a
328 uniform distribution between 10.00 and 12.5 Ma. The minimum age of 10 Ma and the
329 maximum age of 12.5 were based on the appearance of the proposed stem member of the
330 gorilla clade *Nakalipithecus nakayamai*[135,136] and the probable crown pongine
331 *Sivapithecus*[137,138], respectively. Even though there is uncertainty regarding the exact
332 phylogenetic placement of *N. nakayamai*[135,136], we consider that the anatomical features
333 linking it with gorillas are strong enough to use the age associated with this taxon as
334 minimum divergence date for hominines, particularly when considering the possible
335 ancestral-descendent relationship between *N. nakayamai* and the basal gorillin
336 *Chororapithecus abyssinicus*[135,139,140].

We used a normally distributed clock rate prior, with a mean of 0.025 and standard deviation of 0.05, which is consistent with previous estimates of the mitochondrial rate of evolution in humans[141,142]. The Independent Gamma Rate (IGR) relaxed clock model was used for modelling branch rate variation, employing a clock rate variance prior with an exponential distribution of rate 10. We used the FBD model as the prior on divergence times, using an exponential net diversification prior with rate 1, a beta turnover prior with shape parameters α=1 and β=1, a beta fossil sampling proportion prior with shape parameters α=1 and β=1 and an extant sampling proportion of 1. The priors employed in clock rate variance and the FBD model were intentionally diffuse, reflecting the general uncertainty in our prior expectation of the distribution of these parameters.

Even though our main focus was estimating hominin divergence-times, we are aware that that there is still controversy regarding the phylogenetic placement of some of the taxa included in our matrix, particularly in the placement of *Australopithecus sediba*[1,117], *Homo floresiensis*[16,97,98] and *Homo naledi*[17,143]. Therefore, we considered four different topological hypotheses for constraining four independent phylogenetic analyses (Fig. 1): a), a topology similar to the phylogeny of the analysis from which we extracted the morphological data[17]; b), the same topology as a) but moving *Au. sediba* from the *Homo* clade, to be the sister taxa of *Australopithecus africanus* as has been recently suggested[144]; c), the same topology as a) but changing the position of *Homo naledi* from the stem of *Homo antecessor* to be the sister taxa of the African *Homo erectus* as previously suggested[143,145]; d), the same topology of a) but taking *H. floresiensis* from the base of the genus *Homo* to be the sister taxa of the Asian *Homo erectus* as was originally suggested[97]. Nevertheless, we left *H. sapiens*, *H. neanderthalensis, H. heidelbergensis* and Denisovans unconstrained in the four analyses as they had mtDNA sequences which could also be informative of their phylogenetic relationships. Therefore, the constraints we used in all the analyses were soft, so the latter

362 taxa could be accommodated in any position of the tree according their morphological,
363 molecular and stratigraphic information.

364 We performed the analyses with MrBayes 3.2.7a[146] using two runs of four chains and 60
365 million MCMC generations with the first 25% of samples discarded as burn-in. The analyses
366 were run on CIPRES portal v3.3[147]. We ensured that the average standard deviation of split
367 frequencies was below 0.01 and that all parameters had an effective sample size of more than
368 200. Additionally, we visually inspected that the two independent runs achieved convergence
369 and stationarity using the program Tracer v1.7.1[148].

370 **Evaluating the prior sensitivity of divergence-time estimates**

371 In order to evaluate the effect of alternative priors on our divergence-time estimates, we
372 conducted sensitivity analyses in the first tree (i.e., Dembo *et al.*[17] hypothesis) in which we
373 changed the prior distribution of one important model parameter at a time into a reasonable
374 alternative prior distribution, keeping the rest of the model parameters unchanged. This was
375 done for the clock rate variance, the net diversification prior of the FBD model and root age
376 prior. We did this in the former two cases because we wanted to test the effect of using more
377 constrained priors, and in the latter, to account for the possibility that *N. nakayamai* could be
378 a stem hominid before the gorilla–human split[135,136]. Therefore, for the clock rate variance
379 prior, we ran a strict clock and a non-clock analysis constrained to have the same topology.
380 Then, following Ronquist's et al.[25] methodology to estimate rate variance, the clock rate
381 variance prior was estimated as 25.04. For the net diversification prior we followed Zhang *et*
382 *al.*[149] in using an exponential distribution of rate 100. In the case of the root age prior we used
383 a uniform distribution changing the minimum to 8 but keeping the maximum in 12.5 Ma,
384 because of the 8 Ma estimated for appearance of the proposed gorillin *C. abyssinicus*[135,139],

385 which have been used to date the minimum age of the gorilla–human split in previous
386 studies[32,33].

387 **Estimating PEQ using a PGLS regression**

388 The encephalization quotient (EQ) is commonly used to determine how brain size scales with
389 respect to body size for a given individual[48,150–152]. However, EQ does not take into account
390 phylogenetic information, so a newly proposed measurement termed PEQ has been advanced
391 as a way of considering the phylogenetic non-independence between data points[28].

392 Body mass and endocranial volume (ECV) were obtained from the literature (see
393 Supplementary Table 3 for further information). When more than one specimen was
394 available, arithmetic averages for body mass and endocranial volume were used. Endocranial
395 volume was converted into brain mass by dividing ECV by 1.036[153]. We used R version
396 3.6.1[154] and the packages 'ape'[155] and 'nlme'[156] to compute phylogenetic correlations and to
397 fit linear models, respectively. We log-scaled the data, and by assuming a Brownian motion
398 model of evolution we calculated a correlation using the corBrownian() function to then fit a
399 linear model (brain mass was the dependent variable, whilst body mass was the independent
400 one) independently for each one of the four consensus trees obtained in the TED analysis
401 (Extended Data Fig. 8). R^2 were calculated using the R package rr2 v1.0.2 and the function
402 R2.pred()[157]. The resulting equations were used to calculate the expected brain mass (E), and
403 PEQ was calculated as the ratio between the actual estimated brain mass (A) and E (PEQ =
404 A/E) for each one of the living and fossil taxa (Supplementary Table 3).

405 **PEQ and body mass ancestral character state reconstructions**

406 We used a ML approach to perform the ACSR at the internal nodes of the four consensus
407 phylogenetic trees for 1) body mass and 2) PEQ (and brain mass) under a Brownian motion

model. This procedure was performed using the fastAnc() and the contMap() functions from the package 'phytools' v 0.6-99[158]. *Kenyanthropus platyops* and *Australopithecus garhi* tips were dropped from the ACSR for body mass and PEQ as there were no body mass estimations for these taxa available due to their fragmentary fossil record. Similarly, Denisovans were removed from all ACSR analyses as there are no estimates available for their brain and body mass.

Measuring uncertainty in the ML ancestral character state reconstructions

In order to measure the uncertainty in our ML ACSR we sampled every 10th time-calibrated tree from the posterior after discarding the first 25% as burn-in, which it meant a total of 9002 time-calibrated posterior trees sampled for each one of the four analyses. Then we ran ML ACSR analyses in all of these trees and their internal nodes for 1) body mass and 2) PEQ (and brain mass), using the same methods and R packages described in the previous section. For the PEQ ACSR, we previously ran the PGLS analysis for each one of the sampled trees, so the PEQ values in the trees' tips were independently estimated for each tree. This allowed us to incorporate uncertainty in our ACSR, and to analyse if the patterns observed in the ACSR for the consensus trees hold or not when we looked at different trees recovered from the posterior.

Measuring the relationship between ACSR of brain mass and body mass

As brain size increase has been proposed as a driver of body size increase[42], we carried out regressions between our ACSR of brain mass versus body mass in the four consensus trees to test if there was a pattern that could be consistent with that hypothesis. It is important to consider that we did not directly assess the hypothesis a brain size increase drove body mass evolution but rather evaluate if there was a general pattern that could provide further

information about this issue. Both ACSR datasets were log-scaled before performing the regressions.

Data availability

All data analysed in this study are available in the Supplementary information (Supplementary Tables 2 and 3) and in a permanent Zenodo (zenodo.org) repository at https://dx.doi.org/10.5281/zenodo.4537445[159]. Additionally, the data is available in an open access repository at https://github.com/HansPueschel/Hominin-div-time-evolution[159].

Code availability

The code and input files are available in a permanent Zenodo (zenodo.org) repository at https://dx.doi.org/10.5281/zenodo.4537445[159]. In addition, the code and input files are available in as an open access repository at https://github.com/HansPueschel/Hominin-div-time-evolution[159].

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Acknowledgements

This research was funded by the National Agency for Research and Development (ANID)/ PFCHA/Doctorado en el extranjero Becas Chile/2018-72190003 to H.P.P; a Marie Skłodowska-Curie Actions: Individual Fellowship (H2020-MSCA-IF-2018-2020; No. 792611) and the European Research Council (ERC) Starting Grant PalM, under the European

Union's Horizon 2020 Research and Innovation Programme (No. 756226) to O.C.B.; the Leverhulme Trust Early Career Fellowship, ECF-2018-264 to T.A.P.

Author contributions

H.P.P. and T.A.P. conceived and designed the study. O.C.B. compiled the body mass and endocranial volume dataset. J.E.O. provided methodological support. H.P.P. and T.A.P. carried out all the mentioned analyses and wrote an initial draft. H.P.P., O.C.B., J.E.O., R.B. and T.A.P. interpreted the obtained results and contributed to the writing of the submitted version of this work.

Competing interests

The authors declare no competing interests.

Figures

Figure 1. Alternative topological hypotheses tested in the total-evidence dating (TED) analyses. a), similar to the phylogeny of Dembo *et al.*[17]; b), the same topology as a) but moving *Au. sediba* from the *Homo* clade, to be the sister taxa to *Au. africanus*; c), the same topology as a) but changing the position of *H. naledi* from the stem of *H. antecessor* to be the sister taxa to the African *H. erectus*; d), the same topology of a) but taking *H. floresiensis* from the base of the genus *Homo* to be the sister taxa to the Asian *H. erectus*.

Figure 2. Summary diagram of important paleoclimatic and hominin evolution events plotted next to the four obtained consensus phylogenies and time divergence estimates (Red node bars represent the 95% highest posterior density [HPD] for the estimated node ages). a) Dembo *et al.*[17] hypothesis, b) *Au. sediba* hypothesis, c) *H. naledi* hypothesis, and d) *H. floresiensis* hypothesis. A composite benthic foraminifera oxygen isotope record obtained from[53] is displayed at the top of the figure to illustrate the evolution of high-latitude glacial

837 cycles and dominant periodicity of glacial variability, as well as palaeotemperatures (the red
838 line corresponds to a smoothing spline used to depict the main trend in $\delta^{18}O$
839 values; smoothing parameter=0.2).

840 **Figure 3.** Body mass ancestral character state reconstructions (ACSR) for each species
841 mapped onto the four consensus time-calibrated phylogenies. a) Dembo *et al*.[17] hypothesis, b)
842 *Au. sediba* hypothesis, c) *H. naledi* hypothesis, and d) *H. floresiensis* hypothesis. The values
843 at nodes and branches were reconstructed using a maximum-likelihood ancestral character
844 estimation method under a Brownian motion model.

845 **Figure 4.** PEQ ancestral character state reconstructions (ACSR) for each species mapped
846 onto the four consensus time-calibrated phylogenies. a) Dembo *et al*.[17] hypothesis, b) *Au.*
847 *sediba* hypothesis, c) *H. naledi* hypothesis, and d) *H. floresiensis* hypothesis. The values at
848 nodes and branches were reconstructed using a maximum-likelihood ancestral character
849 estimation method under a Brownian motion model.

850 **Figure 5.** Boxplots of a-d) body mass (kg) and e-h) PEQ ancestral character state
851 reconstructions (ACSR) per node based on a sample of 9002 time-calibrated posterior trees
852 for each of the tested hypothesis. a, e) Dembo *et al*.[17] hypothesis, b, f) *Au. sediba* hypothesis,
853 c, g) *H. naledi* hypothesis, and d, h) *H. floresiensis* hypothesis. The red dots indicate the
854 ACSR conducted using the consensus trees. The median is indicated by the horizontal black
855 line, the interquartile range (IQR) is the white box, and the whiskers indicate the minimum
856 and the maximum (at 1.5 * IQR of the lower and upper hinge respectively).

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858

Table 1. Divergence times mean and 95% highest posterior density interval (HPD) in Ma for the different phylogenetic hypotheses in Fig. 1. The maximum and minimum bounds for the 95% HPD are in parentheses. Abbreviations: Div., divergence-times mean; d, Dembo *et al.*[17] hypothesis; s, *Au. sediba* hypothesis; n, *H. naledi* hypothesis; f, *H. floresiensis* hypothesis.

Node*	Div. mean-d	Div. mean-s	Div. mean-n	Div. mean-f
1	10.35 (11.40, 10.00)	10.35 (11.42, 10.00)	10.37 (11.49, 10.00)	10.33 (11.36, 10.00)
2	7.47 (8.52, 6.66)	7.43 (8.43, 6.61)	7.50 (8.59, 6.67)	7.46 (8.53, 6.63)
3	7.20 (8.11, 6.51)	7.15 (8.06, 6.49)	7.22 (8.15, 6.51)	7.18 (8.10, 6.47)
4	6.40 (7.59, 5.21)	6.41 (7.55, 5.26)	6.42 (7.57, 5.24)	6.39 (7.54, 5.21)
5	5.44 (6.49, 4.60)	5.44 (6.42, 4.61)	5.50 (6.52, 4.64)	5.42 (6.47, 4.56)
6	4.90 (5.76, 4.18)	4.97 (5.80, 4.24)	4.95 (5.82, 4.24)	4.87 (5.72, 4.15)
7	3.97 (4.47, 3.63)	3.94 (4.40, 3.62)	3.98 (4.50, 3.63)	3.97 (4.46, 3.62)
8	4.52 (5.32, 3.83)	4.60 (5.41, 3.92)	4.56 (5.37, 3.86)	4.49 (5.29, 3.82)
9	4.06 (4.76, 3.44)	4.12 (4.78, 3.52)	4.09 (4.80, 3.46)	4.02 (4.73, 3.39)
10	3.83 (4.51, 3.19)	3.93 (4.58, 3.34)	3.85 (4.57, 3.19)	3.77 (4.46, 3.13)
11	2.93 (3.34, 2.65)	2.93 (3.33, 2.65)	2.94 (3.36, 2.66)	2.93 (3.34, 2.65)
12	2.47 (2.81, 2.22)	2.46 (2.79, 2.22)	2.48 (2.82, 2.22)	2.47 (2.81, 2.22)
13	3.47 (4.21, 2.75)	3.24 (4.05, 2.59)	3.52 (4.30, 2.81)	**1.73 (2.09, 1.47)**
14	2.94 (3.46, 2.53)	2.81 (3.30, 2.40)	2.98 (3.50, 2.55)	3.04 (3.62, 2.56)
15	2.70 (3.17, 2.35)	**3.57 (4.23, 2.94)**	2.73 (3.21, 2.36)	2.75 (3.25, 2.34)
16	2.63 (3.10, 2.25)	2.54 (2.97, 2.19)	2.67 (3.15, 2.28)	2.70 (3.21, 2.26)
17	2.39 (2.83, 2.02)	2.33 (2.73, 1.99)	2.44 (2.88, 2.06)	2.45 (2.93, 2.05)
18	2.13 (2.54, 1.79)	2.09 (2.47, 1.78)	2.18 (2.58, 1.82)	2.19 (2.63, 1.83)
19	1.89 (2.27, 1.57)	1.87 (2.21, 1.57)	1.91 (2.30, 1.57)	1.98 (2.37, 1.64)
20	1.59 (2.02, 1.20)	1.57 (1.99, 1.20)	**1.94 (2.35, 1.58)**	1.61 (2.06, 1.18)
21	1.42 (1.83, 1.04)	1.42 (1.81, 1.04)	1.62 (2.09, 1.17)	1.43 (1.84, 1.01)
22	1.09 (1.50, 0.73)	1.08 (1.46, 0.74)	1.17 (1.59, 0.76)	1.08 (1.50, 0.70)
23	0.77 (1.13, 0.40)	0.77 (1.12, 0.42)	0.80 (1.20, 0.43)	0.76 (1.16, 0.38)
24	0.60 (1.01, 0.26)	0.59 (0.94, 0.27)	0.63 (1.03, 0.28)	0.59 (1.02, 0.25)

*Node's ages that are not comparable due to the specific changes in the phylogenetic hypotheses are indicated in bold.

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